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The species diversity × fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests

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Abstract. The combination of direct human influences and the effects of climate change are resulting in altered ecological disturbance regimes, and this is especially the case for wildfires. Many regions that historically experienced low–moderate severity fire regimes are seeing increased area burned at high severity as a result of interactions between high fuel loads and climate warming with a number of negative ecological effects. While ecosystem impacts of altered fire regimes have been examined in the literature, little is known of the effects of changing fire regimes on forest understory plant diversity even though understory taxa comprise the vast majority of forest plant species and play vital roles in overall ecosystem function. We examined understory plant diversity across gradients of wildfire severity in eight large wildfires in yellow pine and mixed conifer temperate forests of the Sierra Nevada, California, USA. We found a generally unimodal hump-shaped relationship between local (alpha) plant diversity and fire severity. High-severity burning resulted in lower local diversity as well as some homogenization of the flora at the regional scale. Fire severity class, post-fire litter cover, and annual precipitation were the best predictors of understory species diversity. Our research suggests that increases in fire severity in systems historically characterized by low and moderate severity fire may lead to plant diversity losses. These findings indicate that global patterns of increasing fire size and severity may have important implications for biodiversity.

Key words: climate change; diversity; fire; fire severity; forest; understory plants.

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INTRODUCTION

Ecological disturbances shape and restructure abiotic resources and biotic communities (Pickett et al. 1989, Bond and Van Wilgen 1996, Meurant 2012). Humans have major influences on ecological disturbance processes, and disturbance regimes in particular can be greatly altered by human agency (Taylor and Scholl 2012, van Mantgem et al. 2013, Enright et al. 2014). Fire provides excellent examples of how human influences on disturbance regimes can have major impacts on ecosystem states and processes. Human presence usually increases fire occurrence in ecosystems and may lead to deleterious effects on species and ecosystem components and processes not adapted to or resilient to higher fire frequencies (Bowman et al. 2011, McWethy et al. 2013). However, in some ecosystems, humans have notably reduced natural fire

frequencies. Examples of ecosystems affected in this way include grasslands, savannas, and oak and pine woodlands, which tend to support highly frequent, low-severity fire carried principally in surface fuel layers dominated by herbaceous plants and litter and/or small-diameter woody fuels (Syphard et al. 2007, Safford and Van de Water 2014). In these types of fuel beds, fire can be easily ignited but also easily extinguished. In western North America, semiarid forests dominated by fire-resistant conifers such as ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*P. jeffreyi*) are well-known examples of human-affected ecosystems. Since the early 20th century, many forested areas dominated by these and related species have experienced widespread ecosystem transformations, partly or mostly as a result of a century or more of systematic fire suppression by humans. Fire exclusion typically leads to forest densification, accumulation of dead woody material and surface litter, increases in the densities of fire-intolerant tree species, and a shift to a fire regime characterized by highly infrequent but very severe fire (Stephens and Ruth 2005, Van de Water and Safford 2011, Steel et al. 2015).

These trends threaten the resilience of erstwhile frequent-fire forests because few species are adapted to regenerating after severe fire, which was comparatively rare before Euroamerican settlement of western North America (Welch et al. 2016, Tepley et al. 2017, Shive et al. 2018). The impacts of the changed fire regime on forest structure and the dominant tree species have been intensively studied (North et al. 2016, Safford and Stevens 2017, van Wagtendonk et al. 2018); however, little is known about the effects of the changed fire regime on the shrubs and herbaceous plants that make up the forest understory. Western forests are decidedly poor in tree species, and most biota are found in the understory (Booth 1950, Peet 1978, Halpern and Spies 1995, Barbour et al. 2007). Understory plant species play crucial ecological roles in various ecosystem processes and services including nutrient cycling, soil hydrology, food and forage provision, pollination, and provision of animal habitat (Levine et al. 2003, Gilbert and Lechowicz 2004, Gilliam 2007, Kudo et al. 2008, Kuhn et al. 2011). Understory plant communities are also shaped by ecological disturbance, interactions among plant species, and features of the biophysical environment (Bowman et al. 2009, Belote 2015, Burkle et al. 2015, Stevens et al. 2015, Werner et al., *in press*).

Fire intensity is the amount of heat energy released during burning, and this is the most direct influence fire has on an ecosystem (Keeley 2009). Since actual heat flux is difficult to measure, an imperfect surrogate—fire severity—is usually used to measure fire's impact to the ecosystem. Fire severity is a measure of the effect of fire intensity on the ecosystem driven by interactions between the fire's heat, plant species adaptations, and environmental conditions (Keeley 2009). However, the same amount of energy input can severely impact certain ecosystems but barely affect others, so system recovery and reassembly may vary greatly depending on the severity of fire. Low-severity sites may recover in an auto-successional manner (e.g., Matthews et al. 2018) because while the post-fire system may differ initially in the distribution of fuel loads and some small-statured plant mortality, it is largely similar to or quickly returns to resemble the system it was before fire in terms of overstory species composition, seedbank diversity, nutrient, water and light availability, and so on (Turner et al. 1999, Wang and Kemball 2005). Low-severity sites therefore exhibit a sort of system memory, whereas sites burning at high severity look and function dramatically differently from their prefire state (Sugihara et al. 2006, Shenoy et al. 2013). Features such as living overstory trees and viable seedbanks may be rare to nonexistent in high-severity sites post-fire, and ecosystem-level characteristics such as light infiltration to the understory, soil structure, and nutrient availability are often decidedly altered (Wells et al. 1979, Certini 2005, van Wagtendonk 2006, Stevens et al. 2015).

Fire can increase forest heterogeneity (Collins and Stephens 2010), which can in turn increase species diversity (Harner and Harper 1976, Huston 1994), but progressively larger high-severity burn patches may decrease habitat heterogeneity (Safford and Stevens 2017, Shive et al. 2018, Steel et al. 2018). Such homogenization of the post-fire environment could have major effects on forest biodiversity (Lindner et al. 2010, Hessburg et al. 2016). A rich body of ecological theory posits a variety of potential diversity and disturbance

severity relationships with the shape and amplitude of the diversity response varying based on factors such as ecosystem productivity, the composition of the species pool, evolutionary feedbacks, and the type of disturbance (Grime 1977, Huston 1994, Safford et al. 2001, Safford and Mallek 2011, Hall et al. 2012). Previous research has examined understory community responses to prescribed fires in various North American forest types (Halpern 1989, Schoennagel et al. 2004, Wayman and North 2007, Webster and Halpern 2010). However, such studies are nearly universally restricted to the lower half of the fire severity gradient because prescribed fires are almost always carried out under moderate weather and fuel conditions intended to preclude high-severity burning. Such studies have mostly documented increasing plant species richness or diversity with increasing fire severity with the pattern in the upper half of the fire severity gradient left to the imagination.

Importantly, plant responses to fire severity could be contingent upon historical fire regimes. In a recent review, Miller and Safford (2019) summarized the ecological literature concerning understory plant species response to wildfire from the western United States using only studies that included more than one fire severity class and unburned controls. They were able to locate 13 studies that included the full fire severity gradient. In these studies, they found that plant species richness responses to fire severity depended to a great extent on the historical (e.g., pre-Euroamerican arrival) disturbance regime of the ecosystem in question because it was a fundamental driver of species adaptations and the makeup of the species pool. For instance, in forest types historically defined by frequent, low–moderate severity fires (Fire Regime Group 1 of Schmidt et al. 2002), species richness tended to be unimodal along the fire severity gradient (from unburned to high severity; DeSiervo et al. 2015, Stevens et al. 2015). In contrast, in moist, high elevation forests defined by infrequent, high-severity fires (Fire Regime Groups IV and V), species richness tended to rise with fire severity (Miller and Safford 2019). However, further research is needed to clarify whether these patterns are generalizable.

In this study, we examine plant community responses to fire severity in dry conifer forests that occupy more than 1.7 million km^2 of the United States (Schmidt et al. 2002) and are the site of the most notable increases in fire size and fire severity over the last three decades in the lower 48 states (Safford and Van de Water 2014, Steel et al. 2018). Such dramatic changes in fire regimes at continental scales may pose major threats to the ecosystems affected and the services they provide. In this paper, we seek to generate more robust documentation of the relationship between plant species diversity and fire severity in Fire Regime Group I forests in the western United States and provide an independent test of the patterns reported by Miller and Safford (2019). Working in eight burned areas in yellow pine and mixed conifer (YPMC) forests of the Sierra Nevada, California, we asked two principal questions: (1) How does understory plant species diversity (alpha and gamma) vary along the entire fire severity gradient? and (2) how does fire severity influence the rate of species turnover on the landscape (beta diversity)? Under (1), we hypothesized that local (alpha) and total (gamma) diversity would exhibit a hump-shaped pattern across the fire severity spectrum with low diversity in unburned and high-severity classes and higher diversity in low and moderate-severity classes. Under (2), we expected to find high species turnover among plots in low and moderate-severity classes and less difference between plots in unburned and high-severity classes.

Methods

Study sites

We sampled eight areas (hereafter "fires") in YPMC forests of the Sierra Nevada, California (Fig. 1; Table 1), that were burned in unintentional wildfires. YPMC forests historically supported high-frequency, low-severity fire regimes that have been notably altered by human management over the last century (Safford and Stevens 2017). Yellow pine and mixed conifer forests are the most widespread forest type in the Sierra Nevada, occurring above oak woodlands and mixed evergreen forest and below red fir forests, generally at elevations between 500 and 2000 m. They are dominated by the yellow pines (ponderosa pine [*P. ponderosa* Lawson & C. Lawson] and Jeffrey pine [*P. jeffreyi* Balf.]); white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex

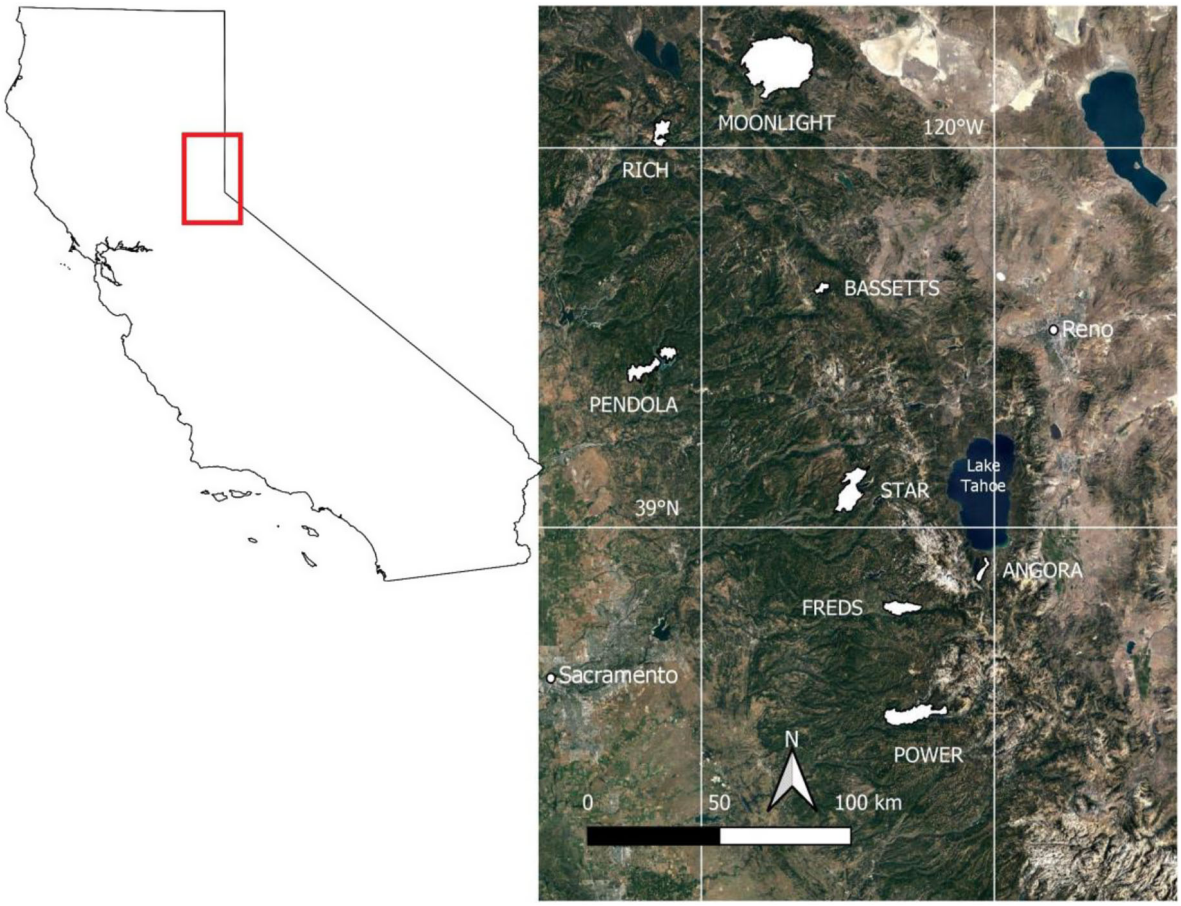

Fig. 1. Locations and areas of fires included in this study.

Hildebr.); sugar pine (*P. lambertiana* Douglas); incense cedar (*Calocedrus decurrens* (Torr.) Florin); Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*); and a number of hardwood species, most notably black oak (*Quercus kelloggii* Newberry) and canyon live oak (*Quercus chrysolepis* Liebm.) (Safford and Stevens 2017). The climate is Mediterranean with warm, dry summers and cold, wet winters. Most of the YPMC forest falls within the Cwb climate zone of Köppen, where the mean temperature of the warmest month is below 22°C, at least 3× more rain falls in the wettest month than in the driest month, and the proportion of rain to snow is >1:1 (Safford and Van de Water 2014).

Sample collection and processing

We chose fires that were of sufficient size to permit location of ≥10 randomly located plots in each of six fire severity classes. We conducted field sampling at least five years post-fire between early May and early August. We located potential plot locations through a stratified random process based on the US Forest Service classification of fire-caused basal area mortality found at https://www.fs.usda.gov/detailfull/r5/landmanagement/resourcemanagement/?cid=STELPRDB5362659. These are based on satellite-measured relative differenced normalized burn ratio calibrated to extensive field data, and they are not subject to the subjective burn severity classification used in the Monitoring Trends in Burn Severity program (Miller and Thode 2007, Miller et al. 2009). We used ArcGIS software to overlay a 400 × 400 m grid across each fire area, and potential plot centers were located at grid nodes. Within each fire severity class in the imagery, at least 10 potential sites were sampled in the field

Table 1. Details of fires sampled including years of ignition and sampling, elevation range, and number of plots surveyed for each fire.

Fire name	Fire abbv.	Burn year	Size (ha)	Year of sampling	Years since fire	Elevation range (m)	Severity class (no. of plots)					
							0	1	2	3	4	5
Angora	ANG	2007	1220	2015	8	1905–2251	29	7	14	14	16	15
Bassetts	BAS	2006	939	2015	9	2129–2741	6	18	2	1	1	6
Freds	FRD	2004	3298	2013	9	1291–2090	10	14	10	2	7	5
Moonlight	MNL	2007	26,595	2014	7	1488–2167	10	6	12	17	15	20
Pendola	PEN	1999	4753	2011	12	598–966	17	17	13	9	10	25
Power	PWR	2004	6987	2014	10	1003–2294	11	13	23	19	26	24
Rich	RCH	2008	2703	2013	5	967–1943	38	8	31	20	22	11
Star	STA	2001	6817	2015	14	1616–2456	0	10	7	4	2	13
Total							121	93	112	86	99	119
Means/range					9	1377–2114	15	12	14	11	12	15

in each fire, but final sample sizes varied due to discrepancies between image and field-based severity assessments and vegetation type mismatches. We used circular, 405-m^2 (1/10 acre) study plots following the Forest Service's Common Stand Exam protocol (USDA Forest Service Region 5, Common Stand Exam Field Guide 2012). To characterize fire severity in the field, we assessed scorch heights, torch heights, and existing vegetation, and we binned study plots into six fire severity classes (Table 2), from Welch et al. (2016). We made ocular estimates of cover for all plant species in each study plot and gave any species with <1% cover a trace designation. We identified plants using The Jepson Manual (Baldwin et al. 2018). We also recorded environmental data including elevation, slope, aspect, total overstory cover, litter depth, and litter cover. Time since fire was derived by subtracting the year of burning from the year of sampling, but because unburned controls were also included, time since last fire for these plots as well as total number of fires over the last 110 yr for every plot was extracted from the US Forest Service Pacific Southwest Region Fire Return Interval Departure GIS database (Safford and Van de Water 2014). We used the basin characterization model (Flint and Flint 2007, 2014) to extract annual climatic water deficit and mean annual precipitation estimates (resolution, 270 m) and generated estimates of heat load and potential direct incident radiation for our plot locations using latitude, aspect, and slope (McCune and Keon 2002, McCune 2007).

Diversity indices

Alpha (local) diversity was measured as local species richness (mean number of species per 405-m^2 plots), and the per plot means of the antilogarithm Shannon diversity index (focus on

Table 2. Fire severity classification used for ground-truthing remotely sensed severity estimates (from Welch et al. 2016).

Fire severity class (designation)	Description	% Basal area mortality
0; unburned	Unburned	0
1; low	Lightly burned, no significant overstory mortality, patchy spatial burn pattern, groups of surviving shrubs/saplings	0–25
2; low–moderate	Lightly burned, isolated overstory mortality, most saplings/shrubs dead	25–50
3; high–moderate	Moderately burned, mixed overstory mortality, understory mortality burned to the ground	50–75
4; high	High intensity, significant proportions (75–100%) of overstory killed, dead needles remaining on trees one year later	75–90
5; high	High-intensity burn, total/near-total mortality of overstory, most needles consumed in fire	>90

rare species, cover as abundance), inverse Simpson index (focus on abundant species, cover as abundance), and Pielou's evenness (cover as abundance), were based on formulas from Pielou (1984) and Ludwig and Reynolds (1988). Data from the eight fires were pooled by severity class for these analyses, but they were also examined on a per fire basis.

Beta (between site) diversity was measured as Jaccard dissimilarity (1-J) between plots within each fire severity class in each fire. The overall means from the eight mean 1-J measures were also calculated for each fire severity class and then pooled into unburned, low severity (class 1), moderate severity (classes 2 and 3), and high severity (classes 4 and 5) for ease of interpretation.

Gamma (total) diversity for each severity class was calculated using averaged rarefied richness from the vegan package (Oksanen et al. 2018) in R statistical software (R Development Core Team 2013). We used 4 as the minimum sample size, and we excluded Bassetts from the analysis because of especially low plot numbers in severity classes 3 and 4.

Statistical analyses

All data were tested for normality and heteroscedasticity of residuals, and data transformations were applied if necessary. One-way ANOVAs were conducted to examine differences in diversity indices, evenness, and dissimilarity among fire severity classes using GraphPad Prism 8.01 software (Motulsky et al. 2017). Tukey multiple-comparison tests were employed after ANOVAs when there were statistically significant differences among fire severity classes.

To determine which species were most characteristic in the understory vegetation of a given fire severity class, two-way indicator species analysis (TWINSPAN) was used in PC-ORD (McCune and Mefford 1999).

To examine the influence of fire severity and other environmental factors on our observed diversity metrics, we used restricted maximum-likelihood linear mixed-effects models from the lme4 package (Bates et al. 2014) in R statistical software (R Development Core Team 2013). For each dependent variable (species richness, antilog Shannon diversity index [AS], Simpson's diversity index [SI], and Pielou's evenness [PE]), we created a full model including our main effect (fire severity; 0–5) and a suite of other environmental variables including year, elevation, slope, aspect, total overstory cover, litter depth, litter cover, time since last fire, number of fires, climatic water deficit, mean annual precipitation, heat load, and potential direct incident radiation, as well as interactions between fire severity and litter cover, litter depth, and overstory cover. Fires were included as a random blocking variable in all of the models. Prior to analysis, we determined whether a polynomial term should be used in each model by examining the diversity metrics across fire severity. Ultimately, a second-order polynomial was applied to fire severity for the curved pattern of species richness, while no polynomial was applied for AS, SI, and PE because they exhibited linear relationships. After running the full model, nonsignificant predictors were eliminated and the model rerun.

Results

Species diversity measures

In our pooled analyses, all of our measures of diversity and evenness showed notable differences across fire severity classes (Figs. 2 and 3). Species richness showed significant differences ($F_{5,\ 623} = 6.292$, $P < 0.0001$) between unburned controls (0) and fire severity classes 2 ($P = 0.034$), 3 ($P < 0001$), and 4 ($P = 0.023$), between fire severity class 1 and class 3 ($P = 0.003$), and

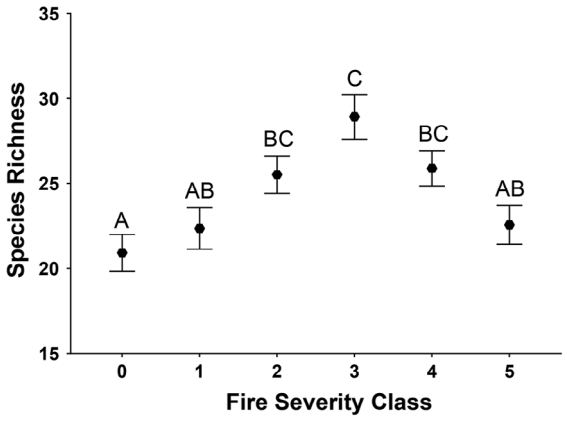

Fig. 2. Species richness of all fires combined across fire severity classes. Means with different letters are significantly different from each other (Tukey test, $P < 0.05$).

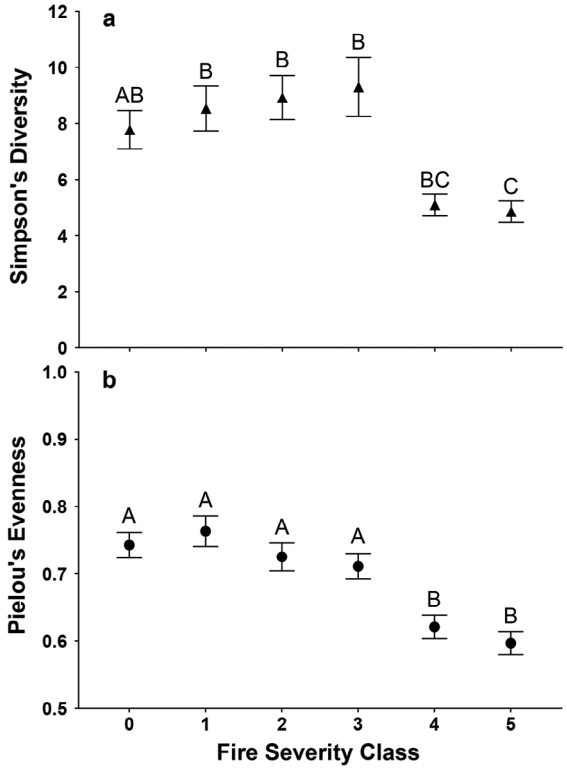

Fig. 3. (a) Simpson diversity index of all fires combined across fire severity classes (overall ANOVA $F_{5,\ 623} = 7.914$, $P < 0.0001$). (b) Pielou's evenness of all fires combined across fire severity classes (overall ANOVA $F_{5,\ 623} = 12.75$, $P < 0.0001$). Means with different letters are significantly different from each other (Tukey test, $P < 0.05$).

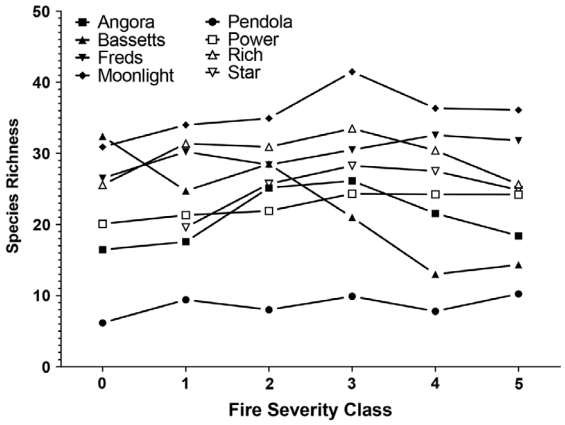

Fig. 4. Plant species richness vs. fire severity relationships for the eight fires included in this study. Solid squares are data from Angora Fire; solid right-side up triangles are data from Bassetts Fire; solid upside-down triangles are data from Freds Fire; solid diamonds are data from Moonlight Fire; solid circles are data from Pendola Fire; open squares are data from Power Fire; open right-side up triangles are data from Rich Fire; and open upside-down triangles are data from Star Fire.

between fire severity class 3 and class 5 ($P = 0.002$; Fig. 2). We found 602 unique plant species, and we have provided a complete species list (Appendix S1). Patterns of the diversity vs. severity relationship varied somewhat among fires. As an example, we show the richness x severity relationship for each fire in Fig. 4. Five of the fires showed peaks in richness at moderate severity (hump-shaped relationships), and one fire each showed a positive plateau (Freds), a negative trend (Bassett's), and no relationship (Pendola; Fig. 4).

The two diversity indices and evenness all showed the same general pattern: similar (or slightly rising) diversity from unburned to fire severity class 3, and then a major drop in the high-severity classes 4 and 5. We show Simpson's and Pielou's indices in Fig. 3 (antilog Shannon diversity indices—nearly identical pattern to Simpson's—were also significantly different across fire severity classes at $P < 0.0001$) (Appendix S2: Fig. S2).

Mean gamma diversity (as rarefied richness) displayed a hump-shaped relationship with fire severity (Fig. 5) similar to that of alpha diversity. While unburned controls were not significantly different from the highest severity class (5), their gamma diversity was decidedly lower than understory communities in low to moderate severity (2, $P = 0.016$; 3, $P < 0.0001$; and 4, $P = 0.0005$). Overall, understory communities in severity class 3 showed significantly higher gamma diversity than plots anywhere else along the spectrum ($P < 0.0001$ for all).

The average species dissimilarity among plots in our unburned class was higher than in any of the burned classes (Fig. 6). Dissimilarity dropped slightly at higher severities, and when blocked as with gamma diversity, the highest values were found in the unburned and low-severity classes, medium values in the moderate-severity classes, and lowest values in the high-severity classes.

Fig. 5. Gamma diversity as rarefied richness for all fires combined across fire severity classes (overall ANOVA $F_{5,33} = 27.06$, $P < 0.0001$). Means with different letters are significantly different from each other (Tukey test, $P < 0.05$).

However, our analyses did not reveal any of these fire severity blocks to be statistically significant from each other.

Species indicator analyses

Analysis of the dataset with TWINSPAN derived three conifer tree species (*P. ponderosa*, *P. lambertiana*, and *C. decurrens*; present in the understory as seedlings) as reliable indicators ($p < 0.05$) for the unburned, low and low–moderate severity classes. The fire-stimulated shrubs *Ceanothus integerrimus* and *C. cordulatus* were significant indicators of high–moderate and high-severity burning.

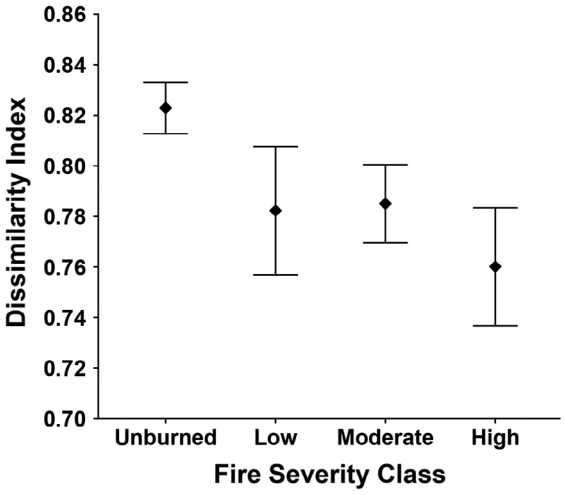

Fig. 6. Dissimilarity for all fires combined and blocked into unburned (fire severity class 0); low (fire severity class 1); moderate (fire severity classes 2 and 3); and high (fire severity classes 4 and 5).

Influence of fire severity and environmental variables on diversity indices

A small set of environmental variables (fire severity, time since last fire, elevation, litter cover, litter depth, overstory cover, and mean annual precipitation) were significant predictors of understory plant species richness, diversity, and evenness but varied depending on the particular index (Table 3). Fire severity (unimodal relationship with richness, negative with the other dependent variables) and litter cover (mostly negative relationship, but marginally significant positive relationship with richness) were the only two predictor variables that appeared in all of our models. Mean annual precipitation (negative relationship with the dependent variables) appeared in the models for richness and diversity; overstory cover (positive relationship) appeared in the models for diversity and evenness (Table 3). Time since last fire was negatively related to diversity, wherein older fires were less diverse. Higher elevations supported lower species richness overall. In the model for richness, there was a significant interaction between elevation and precipitation, such that at lower elevations, richness declined with increasing precipitation while at higher elevations greater precipitation led to more understory species. Year of sampling helped to explain some of the differences in richness between fires but did not prove to be an important predictor of the relationships between richness, diversity, or evenness and fire severity. Our best model for species richness explained 61% of the variance, and our best Shannon index model explained 50%; models for the two other diversity measures did not account for a majority of the variance in the dependent variables (Table 3).

Discussion

We found that post-wildfire understory plant richness and diversity in forest types historically characterized by frequent, low-severity fire exhibit a unimodal pattern along the fire severity

Table 3. Linear mixed-effects models for predicting species richness, antilog Shannon diversity index, Simpson diversity index, and Pielou's evenness.

Dependent variable	Fixed effects	Coefficient	SE	*t* Value	*P*-value
Species Richness	(Intercept)	0.959	0.110	8.706	<0.001
	Fire severity^2	−0.007	0.002	−3.272	0.001
	Elevation	−0.402	0.187	−3.606	0.032
	Litter depth	−0.181	0.054	−3.355	<0.001
	Litter cover	0.044	0.023	1.896	0.058
	Mean annual precipitation	−0.888	0.147	−6.035	<0.001
	Elevation* precipitation	0.869	0.257	3.386	<0.001
Antilog Shannon Diversity Index	(Intercept)	0.933	0.086	10.846	<0.001
	Fire severity	−0.015	0.005	−3.036	0.003
	Time since last fire	−0.118	0.043	−2.765	0.006
	Overstory cover	0.080	0.027	2.926	0.004
	Litter cover	−0.045	0.023	−1.936	0.053
	Mean annual precipitation	−0.283	0.087	−3.253	0.001
Simpson's Diversity Index	(Intercept)	−0.753	0.035	−21.49	<0.001
	Fire severity	−0.006	0.002	−2.741	0.006
	Time since last fire	−0.049	0.019	−2.557	0.003
	Overstory cover	0.037	0.012	3.018	0.003
	Litter cover	−0.024	0.010	−2.317	0.021
	Mean annual precipitation	−0.087	0.037	−2.315	0.023
Pielou's Evenness	(Intercept)	0.465	0.040	11.551	<0.001
	Fire severity	−0.019	0.009	−2.115	0.032
	Overstory cover	0.122	0.044	2.799	0.005
	Litter cover	−0.103	0.037	−2.751	0.006

Note: Random effect for all models is Fire ID, and additional model attributes (R^2, AIC, variance) are as follows: species richness (R^2, 0.61; AIC, −570.44; variance, 0.009); antilog Shannon (R^2, 0.50; AIC, −574.68, variance, 0.013); Simpson's diversity (R^2, 0.40; AIC, −1423.31; variance, 0.0002); and Pielou's evenness (R^2, 0.28; AIC, −567.22; variance, 0.004).

gradient. Across our eight study fires, understory plant species richness and total diversity were highest in moderate fire severity classes and lowest in the unburned and high-severity classes. Our other diversity and evenness measures showed similar but less accentuated patterns. These findings generally correspond to the unimodal hump-shaped relationship between diversity and disturbance described in the theoretical literature for ecosystems of moderate levels of ecosystem productivity (Connell 1978, Huston 1994, Hall et al. 2012). Higher levels of post-fire diversity in areas burned at moderate severity were also found in dry forests by DeSiervo et al. (2015) and Stevens et al. (2015), and there is evidence that this may be a general pattern for forests adapted to frequent, low-severity fire (Miller and Safford 2019). Our results thus further confirm the generality of the hump-shaped diversity vs. fire severity pattern in FRG I forests.

The drop in diversity at high levels of severity in YPMC forests (and other similar ecosystems adapted to frequent, low- and moderate-severity fire) is likely due to a number of factors: (1) There is a general lack of species with adaptations to survive and/or regenerate (e.g., fire-cued germination and serotiny) after high-severity fire in communities adapted to primarily low-severity fire regimes (Grubb 1977, Denslow 1985, Keeley and Safford 2016); (2) those relatively few species in the Sierra Nevada that do respond positively to high-intensity fire include a group of widespread, highly competitive shrubs (mostly in the genus *Ceanothus*) that rapidly dominate high-severity burn patches and competitively exclude conifer seedlings and many herbaceous species (Bohlman et al. 2016, Welch et al. 2016); and (3) the altered (warmer, drier) environmental conditions associated with severely burned sites can filter out species adapted to more mesic habitat conditions, especially in regions with hot, dry summers such as California (Stevens et al. 2015, Keeley and Safford 2016, Miller and Safford 2019).

Both theoretical evidence and empirical evidence suggest that high-severity disturbances should generally homogenize biota, because

relatively few species can survive such conditions (Connell 1978, Huston 1994, Grime 2006); such an effect should be exaggerated in ecosystems with little evolutionary exposure to high-severity disturbance. We found evidence for this effect, as diversity and evenness measures all dropped in the high-severity classes, and our diversity between sites (beta) and total diversity measures were also low in the high-severity classes. On the other end of the fire severity spectrum, unburned forest plots also tended to support lower levels of alpha diversity and the overall species pool (gamma diversity) was similarly low in the high-severity plots. Dry forests that have experienced long-term fire exclusion (75% of YPMC forests in California have not experienced a single fire in >100 yr; Steel et al. 2015) are typically dominated by dense canopies of shade-tolerant conifers and thick layers of surface litter where little light reaches the forest floor and understory diversity is typically low (North et al. 2016, Safford and Stevens 2017). When such long unburned forests are burned at low to moderate severity, our results suggest that plant species richness and diversity benefit, at both the local (alpha) and regional (gamma) scale. Where such forests burn at high severity—which is increasingly more likely under contemporary fuel and climate conditions (Steel et al. 2015, Safford and Stevens 2017, Restaino and Safford 2018)—plant richness does not benefit and diversity and evenness (i.e., taking into account abundance relationships) decline.

While moderate levels of burning are often perceived as a driver of heterogeneity, we also observed relatively high between site diversity in unburned areas. Our unburned plots are necessarily found mostly around the perimeter of the sampled fires, and many are thus separated by notably more distance than the plots in other severity classes. We suspect this is inflating species turnover between plots in the unburned class, so we conducted a Mantel test comparing species dissimilarity and geographic distance among our plots in PC-ORD (McCune and Mefford 1999) and confirmed that they were indeed significantly correlated.

Our findings of reduced understory diversity in high-severity sites imply the potential for declines in landscape species richness with changing fire regimes. Areas burned at higher levels of fire severity in dry forests such as our YPMC sites support fewer plant species, lower levels of diversity, lower evenness, and less dissimilarity across the landscape (Savage and Mast 2005, Strom and Fule 2007, Guiterman et al. 2018). Thus, the shift from the historical high-frequency/low-severity fire regime (FRG I) to the modern low-frequency/high-severity fire regime (FRG III and FRG IV) is reducing both local and landscape-level plant diversity. Under current fire patterns in dry forests, the landscape area dominated by low-diversity high-severity burn patches/shrub fields is increasing rapidly and often transitions to persistent shrublands and potentially stable states of montane chaparral (Miller and Safford 2012, Mallek et al. 2013, Steel et al. 2015, 2018, Coppoletta et al. 2016). Because montane chaparral is characterized by a different natural fire regime (low frequency/high severity) than YPMC forest, re-entry of fire into these shrub fields generally kills tree seedlings and saplings that have colonized since the original burn. Under climate change and a continuation or acceleration of current fire trends, there is a real possibility that large portions of the Sierra Nevada landscape could be caught in a feedback-loop, threshold-type dynamic of persistent montane chaparral that prevents recovery of former forest in many high-severity burn patches (Coppoletta et al. 2016, Tepley et al. 2017, Dettinger et al. 2018, Restaino and Safford 2018). This could have major effects—not necessarily all negative—on plant and animal diversity and composition (McKenzie et al. 2004, Mallek et al. 2013, Bohlman et al. 2016, White et al. 2016, Miller et al. 2018). It is also worth noting that understory plant diversity loss as a result of persistent montane chaparral and other characteristics associated with high severity could have other important implications that manifest in ecosystem services as reduced nutrient availability and disrupted soil hydrology (e.g., higher erosion rates and sediment input into reservoirs) as well as food and forage provisioning (Wells et al. 1979, Moody and Martin 2004, van Wagtendonk 2006, Stevens et al. 2015).

Fire severity and litter cover were consistently the strongest predictors of patterns in our richness, diversity, and evenness measures. We discussed severity in depth above. As expected, higher litter cover led to lower understory diversity, but had a marginally significant positive

relationship with species richness. We suspect this is due to litter cover acting as much as well as its interactions with other variables in the regression, especially fire severity (which had reversing relationships with species richness in the low- and high-severity classes) and time since last fire. Higher precipitation was associated with lower understory richness, diversity, and evenness, most likely because precipitation is closely correlated with vegetation productivity in semiarid areas (Fites-Kaufman et al. 2007) and recovery of woody plants and canopy closure is much higher in burned wet areas than in burned dry areas. In a similar fashion, older fires supported fewer understory species, most probably because post-fire shrub response has driven down herbaceous diversity in these sites (Bohlman et al. 2016). The positive relationship between overstory cover and understory diversity and evenness is likely due to the reduction in shrub cover that occurs as tree canopies expand, as well as the general amelioration of evaporative stress. In the Sierra Nevada forests we sampled, even in unburned plots, canopy cover >60% is relatively rare and increasing tree cover to about 40–50% total cover in burned sites and low cover in unburned sites can facilitate the coexistence of understory (and epiphytic) species from plant lineages adapted to both mesic and xeric habitats (Stevens et al. 2015, Miller et al. 2018).

All of our fires were sampled at least five years after fire, and all of the sampling occurred during the recent California drought (Griffin and Anchukaitis 2014). Some ruderal species are known to persist only short periods after disturbance, and therefore, we may have missed a few ephemeral species in our sampling (Grime 1977). Additionally, by sampling during an extended drought, the potential exists that we may have undercounted perennial species as some may not have emerged due to lack of soil water (Madsen et al. 2012). Overall, we may therefore have undercounted the total potential number of species in our eight fires, but the drought was of similar severity throughout our sampling area, so we see no reason to suspect bias in our species counts.

Management implications

The post-fire successional trajectory of dry forests is a major management concern as climates continue to warm, dry seasons get drier, and the probability of short-interval reburns becomes more common. Severely burned areas in low and middle elevation California forests are at high risk of (semi)permanent conversion to shrubs in the event of another high-severity fire before forest cover has been able to re-establish (Coppoletta et al. 2016, Tepley et al. 2017). Taken in concert with other recent studies from California (e.g., DeSiervo et al. 2015, Stevens et al. 2015, Bohlman et al. 2016, Welch et al. 2016, Steel et al. 2018), our data show that the conversion of large areas of Sierra Nevada YPMC forest to shrublands by way of high-severity burning is likely to have a negative effect on plant species diversity.

Both forest and fire management practices can have major effects on the occurrence and outcome of fire in FRG I forests in the western United States. Long-term fire suppression in these fire-dependent ecosystems has greatly reduced fire occurrence but ironically increased the probability that the outcomes of fire will be ecologically negative when they occur (Steel et al. 2015). Restoration of low tree densities and low fuel loadings in FRG I forests by managers can greatly increase forest resilience to fire and drought and benefit a suite of forest conditions, ecological processes, and biota (Schwilk et al. 2009, Stevens et al. 2014, Hanberry et al. 2015, Winford et al. 2015). However, the spatial footprint of active management will continue to be limited by economic, ecological, social, and political factors. Restoration of low and moderate-severity fire as an ecological process has the potential to positively affect much larger landscapes (North 2012, Mallek et al. 2013). In FRG I ecosystems such as the forests we studied in California, resilience to rapidly changing environmental conditions will be best promoted by a multifaceted approach that combines strategic forest thinning with a major expansion of prescribed burning and managed wildland fire under moderate weather conditions.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2882/full